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Casuarina: biogeography and ecology of an important tree genus in a changing world

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Abstract Important insights on the invasion ecology of woody plants are emerging from the study of model groups, but it is important to test how widely such results can be generalised. We examined whether drivers of introduction and invasion in the genus *Casuarina* are similar to those identified for other groups. We reviewed the literature, mapped current global distributions, and modelled the potential global distribution of the genus. We assessed the rationale behind introductions, impacts of invasions, and the evolution of management approaches. Casuarinas have been introduced to about 150 countries. Ten of the 14 species in the genus have been introduced outside their native ranges, but only three species are recorded as naturalized or invasive (*C. equisetifolia*, *C. cunninghamiana* and *C. glauca*). Species with large native ranges are more likely to be introduced, and the three invasive species have the largest native ranges and the most records of introduction. There were no clear relationships between life-history traits (e.g. seed mass, plant height, or resprouting ability) and the extent of invasion. About 8 % of the Earth's land surface is potentially suitable for casuarinas and large-scale plantings in some climatically suitable areas have not yet resulted in large-scale invasions; there is a substantial global *Casuarina* invasion debt. Experiences in Florida and the Mascarene Islands highlight that casuarinas have the potential to transform ecosystems with significant control costs. The challenge is to develop management approaches that minimise the impacts of invasions while preserving economic, environmental and cultural values of species in their introduced ranges.

Keywords Biological invasions · *Casuarina* · Ecology · Introduction · Native range · Management · Tree invasions

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Introduction

Species from all taxonomic groups are being moved around the world accidentally and intentionally by humans at unprecedented rates (Ricciardi 2006; Wilson et al. 2009). Many of these organisms have notable

benefits to humans, but some have undesirable consequences in parts of their introduced ranges (McNeely 2001). As human populations grow and concerns regarding the sustainability of different forms of land use increase, more attention is being given to evaluating both the costs and benefits of introduced species. Some introduced species spread from sites of introduction to invade ecosystems where their presence may alter the structure and functioning of such ecosystems. In some cases, such invasive species bring about changes that are deemed undesirable and which may cause widespread degradation of ecosystems resulting in substantial costs (Pyšek and Richardson 2010).

Important insights have emerged in recent decades on many aspects of the numerous processes that determine which organisms are moved by humans and how they are moved and disseminated, the features of species and environments that facilitate establishment, proliferation and spread, and the many facets that need to be considered when attempting to manage introduced species (Richardson 2011). Much work has focussed on trying to understand the full range of processes involved in the movement of woody plant species around the world (Richardson and Rejmánek 2004, 2011), their performance as alien species (Rejmánek and Richardson 1996), and on developing effective management methods (e.g. Richardson 1998; Wilson et al. 2011). Trees did not, however, feature prominently on lists of the most problematic invasive species until recently (Richardson and Rejmánek 2011). But, following the widespread transport and use of thousands of tree species for many purposes in all parts of the world in the past few centuries, the phenomenon of widespread invasions of alien trees is rapidly increasing in importance (Richardson et al. 2008; Richardson and Rejmánek 2011). Comparisons between the performances of species in different situations around the world is important for developing protocols for screening new introductions for invasiveness and for managing species that may become or have already become invasive (Richardson et al. 2008; Simberloff et al. 2010).

Global syntheses of the invasion ecology of particular genera or groups (Richardson and Bond 1991; Richardson and Rejmánek 2004; Williamson and Smith 2007; Dogra et al. 2010; Richardson et al. 2011) have considerable value because: invasiveness in one part of the world is possibly the best predictor of likely invasiveness in climatically similar regions (Richardson and Rejmánek 2004; Hulme 2012); each planting in a new locality represents a test of the determinants of invasiveness and invasibility (Richardson et al. 1994,); and management lessons in one area can be transferred to other regions (e.g. Richardson et al. 2008; Wilson et al. 2011). It is important to consider whether such comparisons yield broad generalities or whether generalisations apply only to a subset of model taxa.

The genus *Casuarina* represents an interesting case study. Like other genera of trees that have been widely planted outside their native ranges (notably *Acacia*, *Eucalyptus* and *Pinus*; Richardson 1998), the global distribution of the genus *Casuarina* has been radically changed by humans in the last few centuries. Unlike the aforementioned genera, no attempt has been made to assess the stage of the global transplant experiment for *Casuarina*, nor the status of each species in terms of naturalization and invasion. The distinct evolutionary lineage of Casuarinaceae (a Gondwanan family with a unique combination of morphological characters; Steane et al. 2003), its widespread distribution, and the economic and ecological significance of its species, makes it an important lineage to compare to existing model taxa. Research on this genus may therefore help to uncover patterns, processes and invasion risks that are not well represented in better studied model groups. Using *Casuarina* species as a model group, we explore the following questions: How far advanced is the natural experiment of global introductions compared to that for other model groups? Do features of the native range tell us anything about potential invasiveness? Does the link between planting intensity and degree of invasion in casuarinas differ from that of Australian acacias, eucalypts and pines? Does a large introduced range coupled with key life-history traits predispose some casuarinas to become naturalized in their new ranges? Are casuarinas likely to become more widespread invaders and appear on lists of invasive species in many more areas in the future?

Casuarinas at home

Species in the genus *Casuarina*, commonly known as casuarinas, beefwoods, she-oaks, Australian pines or ironwoods, are fast-growing evergreen trees native to

Australia, Southeast Asia and the Pacific archipelagos (Wheeler et al. 2011). The family Casuarinaceae includes 4 genera and about 96 species (Wilson 1997; Steane et al. 2003). The number of species in the genus *Casuarina* has been widely debated in the literature. Torrey and Berg (1988) recognized 16 species in the genus, but more recent studies have accepted 17 valid species (Steane et al. 2003; Chezhian et al. 2009; Gaskin et al. 2009; Taylor et al. 2010; Ogunwande et al. 2011; Wheeler et al. 2011), while Boland et al.'s (1996) treatment, in agreement with those of Zhongze and Torrey (1985) and Savourie and Lim (1991), recognize 15 taxa: 11 full species, four of which have two subspecies each. In this paper we use the treatment presented in The Plant List (2010)—currently the most comprehensive and authoritative list for plant names (Kalwij 2012). The 19 taxa, including 14 species, are listed in Table 1.

Casuarina equisetifolia has the largest native range of the species in the genus (Parrotta 1993), and occurs in coastal regions of Northern Australia, Malaysia and Southeast Asia, and Oceania (Parrotta 1993; Rogers and Gamble 2008; Swearingen 1997). It is mostly confined to a narrow strip adjacent to sandy coasts, rarely extending inland. *Casuarina cunninghamiana* has an extensive native range in temperate and subtropical areas along the eastern and northern coasts of Australia. Its ability to withstand periodic inundation makes it important for protecting river banks from erosion (U.S. National Research Council 1984). The native range of *C. glauca* is narrower, extending along the eastern coast of Australia from New South Wales to Queensland (Blombery 1977; Boland et al. 1984). *Casuarina cristata*, native to eastern Australia, occurs in woodlands and open forests. It is a valued source of shade, shelter, timber, and as emergency drought fodder (U.S. National Research Council 1984). *Casuarina obesa* is common in southern Western Australia, but also occurs in central South Australia, north western Victoria and south western New South Wales (Emmott and Greening Western Australia 2001). In southern Western Australia, it has been used extensively to revegetate saline and waterlogged areas. *Casuarina pauper* (closely related to *C. cristata*) is native to southern Australia where it is usually found growing with Slender Cypress-pine (*Callitris gracilis*) in open woodlands on sandy rises (Victorian Resources Online 2011). It produces a very dense wood suitable for fencing, fuel and wood-turning.

Table 1 *Casuarina* taxonomy as used in this paper (derived from The Plant List 2010)

	Casuarina species
1	*C. collina* Poiss. ex Pancher and Sebert
2	*C. cristata* Miq.
	C. cristata subsp. *cristata*[a]
	C. cristata subsp. *pauper*[a]
3	*C. cunninghamiana* Miq.
	C. cunninghamiana subsp. *cunninghamiana*
	C. cunninghamiana subsp. *miodon*
4	*C. equisetifolia* L.
	C. equisetifolia subsp. *incana* (Benth.) L.A.S. Johnson
	C. equisetifolia subsp. *equisetifolia*
5	*C. glauca* Sieber ex Spreng.
6	*C. grandis* L.A.S. Johnson
7	*C. junghuhniana* Miq.
	C. junghuhniana subsp. *timorensis*[a]
	C. junghuhniana subsp. *junghuhniana*[a]
8	*C. obesa* Miq.
9	*C. oligodon* L.A.S. Johnson
	C. oligodon subsp. *abbreviata*[a]
	C. oligodon subsp. *oligodon*[a]
10	*C. orophila* L.A.S. Johnson
11	*C. pauper* F. Muell. ex L.A.S. Johnson
12	*C. potamophila* Schltr.
13	*C. tenella* Schltr.
14	*C. teres* Schltr.

[a] Taxa which have an unresolved taxonomy as listed by the World Checklists for Selected Plant Families (WCSP 2010)

Casuarina junghuhniana is native to Indonesia where it grows naturally on the slopes of volcanoes and is a pioneer species of deforested land (Orwa et al. 2009). It is drought-tolerant and can survive prolonged waterlogging due to its ability to tolerate oxygen deficiency (Orwa et al. 2009). *Casuarina grandis*, native to Papua New Guinea, forms dense stands along rivers and regenerates on gravel banks and open sites (U.S. National Research Council 1984). *Casuarina oligodon*, native to Indonesia and Papua New Guinea (Bourke 1985), occurs at high elevations where it forms extensive pure stands along river beds and on ridge tops (U.S. National Research Council 1984). It is widely used as a windbreak in its natural range where it is often planted around villages to provide protection against strong winds (Orwa et al. 2009). It is a popular subsistence crop for food gardens as well as a fallow

intercrop (Vergara and Nair 1985). *Casuarina orophila*, also native to Papua New Guinea, is not mentioned in the literature. *Casuarina collina* is native to New Caledonia (Gauthier et al. 1999). Natural stands often occur in riparian ecosystems, but the species is abundant on a wide range of soils (Gauthier et al. 1999). This fire-resistant species can quickly colonise disturbed areas (Gauthier et al. 1999). For these reasons, *C. collina* has a high potential for rehabilitation of degraded lands in New Caledonia where nickel mining generates large areas of sterile and toxic lands (Gauthier et al. 1999). Other *Casuarina* species native to New Caledonia not mentioned in the literature include *C. potamophila*, *C. tenella and C. teres*.

The phylogenetic and biogeographic relationships of the genus are complex. A phylogenetic study of Casuarinaceae placed all species native to Australia (*C. cristata*, *C. cunninghamiana*, *C. glauca*, *C. obesa* and *C. pauper*) in the same clade, while the species with native ranges extending further north (Indo-Malesia, New Caledonia and Papua New Guinea) were grouped into the same clade (Steane et al. 2003). Although the native range of *C. equisetifolia* (a coastal species) remains uncertain (Elevitch 2006), natural dispersal methods (e.g. sea-drift) may explain its wide distribution. The grouping of *C. equisetifolia* with Indo-Malesian species (*C. collina*), rather than the endemic Australian species, suggests that *C. equisetifolia* is either a relatively new species that established in Australia from Indo-Malesia, or one that evolved in Australia from a shared ancestor with other Indo-Malesian taxa and then dispersed to other regions (Steane et al. 2003). *Casuarina oligodon* forms a separate clade.

Casuarina species are valued and protected trees in their native range for evolutionary, biodiversity and cultural reasons (Boland et al. 1984). The bark of some species is used by Australian aborigines to construct canoes (Flannery 1999). Some vegetation types dominated by *Casuarina* are of high priority for conservation, e.g. the threatened Belah and Coolibah woodland habitat comprising *C. cristata*, *Eucalyptus coolabah* and *Muehlenbeckia cunninghamii*. Casuarinas also form important habitat for rare animals. For example, the vulnerable Glossy black cockatoo (*Calyptorhynchus lathami*) and the Red-winged parrot (*Aprosmictus erythropterus*) inhabit eucalypt and *C. cunninghamiana* woodlands of which only 25 % remains (Joseph 1982; Chapman 2007). *Casuarina cunninghamiana* woodlands are also an important habitat for the critically endangered Regent Honeyeater (*Anthochaera phrygia*) (Menkhorst et al. 1999). Casuarinas also provide important habitat for the vulnerable Black Grass Dart butterfly, *Ocybadistes knightorum* Lambkin and Donaldson (Lepidoptera: Hesperiidae; Sands and New 2002) and are hosts for various epiphytic orchids (Blombery 1977). Although widespread in southern Western Australia, *C. obesa* has listed as threatened in Victoria under the Flora and Fauna Guarantee Act 1988 (Blake 2009).

The current global distribution of casuarinas

Because of the economic importance of many *Casuarina* species (Fig. 1), they have been introduced to areas around the world where some species have become naturalized or invasive (Fig. 2). The Australian Tree Seed Centre (ATSC) played a major role in the collection, storage and dissemination of *Casuarina* seeds from the 1980s onwards (Midgley 1990). During the 1980s, seedlots of casuarinas were dispatched to a total of 103 countries. The main recipients were Asia (35 % of all seed-lots); Australia (23 %); Africa (19 %); Central and South America (8 %); North America (5 %); South Pacific (3 %); Middle East (2 %) and Indian Ocean Islands (1 %). Most of this seed was distributed to Australia, Bangladesh, Brazil, China, Egypt, India, Kenya, Pakistan, Philippines, Thailand and USA (Midgley 1990). ATSC focussed on seven species: *C. cunninghamiana*—85 countries; *C. equisetifolia*—68; *C. glauca*—66; *C. cristata*—51; *C. obesa*—43; *C. junghuhniana*—17; and *C. oligodon*—15 (Midgley 1990). The percentage of *Casuarina* seed dispatched from the ATSC is likely to have decreased from this time due to an increased demand for other genera and a growing preference for a few *Casuarina* species, notably *C. cunninghamiana*, *C. equisetifolia*, *C. glauca* and *C. obesa*. In the past, the ATSC has been unable to meet the demand for high priority, non-Australian species such as *C. junghuhniana*, *C. grandis* and *C. oligodon* (Midgley 1990). Appendix S1 in Electronic Supplementary Material shows dates of introduction and large-scale cultivation for all *Casuarina* species around the world.

The species richness of *Casuarina* around the world was mapped at a resolution of 15 × 15 decimal degrees

Fig. 1 Examples of uses for *Casuarina* species around the world. **a** The mining company Richards Bay Minerals (RBM) uses *C. equisetifolia* as part of their rehabilitation programme in KwaZulu-Natal, South Africa (photograph: LJ Potgieter). **b** *C. equisetifolia* planted along the beach of Cape Vidal, KwaZulu-Natal, South Africa, for dune stabilisation and shade (photograph: LJ Potgieter). **c** *C. equisetifolia* used for ornament in KwaZulu-Natal, South Africa (photograph: LJ Potgieter). **d** *C. equisetifolia* used for charcoal production at RBM, South Africa (photograph: LJ Potgieter). **e** *C. equisetifolia* planted for drift-sand reclamation on the beach of St. Lucia, KwaZulu-Natal, South Africa (photograph: LJ Potgieter). **f** *C. cunninghamiana* planted as a windbreak in Florida, USA (photograph: GS Wheeler). **g** *C. oligodon* planted with coffee in Mount Hagen, Papua New Guinea (photograph: S Midgley). **h** *C. equisetifolia* used as poles in Tamil Nadu, India (photograph: T Maari). **i** *C. equisetifolia* plantation used as a barrier from salt spray, pollution and wind in Batticaloa, Sri Lanka (photograph: Science Navigators). **j** *C. equisetifolia* cultivated for pulp and paper in Andhra Pradesh, India (photograph: JK Jain). **k** Locals harvesting *C. equisetifolia* in Andrha Prades, India (photograph: S Midgley). **l** Use of *Casuarina* in construction (photograph: P Visser)

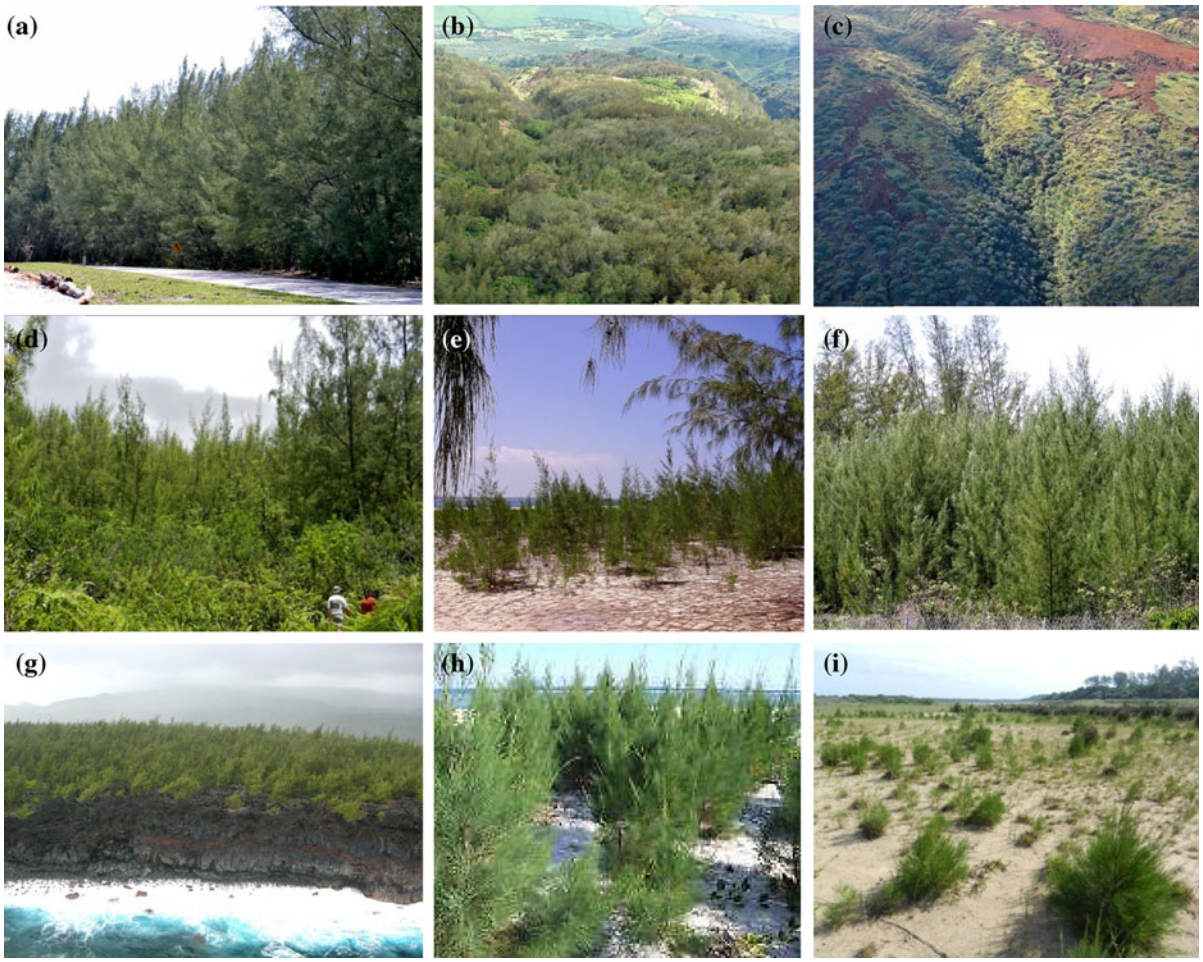

Fig. 2 Examples of landscapes invaded by *Casuarina* species in different parts of the world. **a** *C. equisetifolia* invading along a road in Florida, USA (photograph: GS Wheeler). **b** Dense stands of self-sown *C. glauca* spreading in Hanaula (Maui), Hawaii (photograph: F and K Starr). **c** *C. glauca* invading Kapapa, Oahu, Hawaii (photograph: F and K Starr—fstarr@hawaii.rr.com). **d** Spectacular invasion of *C. equisetifolia* on lava flows, La Réunion Island, southern Indian Ocean (photograph: LJ Potgieter). **e** *C. equisetifolia* saplings invading the coastline of Mbudya Island, Tanzania (photograph: A Witt). **f** Dense stand of *C. equisetifolia* saplings in Florida, USA (photograph: GS Wheeler). **g** *C. equisetifolia* invading Hana (Maui), Hawaii (photograph: F and K Starr). **h** *C. equisetifolia* invading the Cayman Islands (photograph: C Clubbe). **i** *C. equisetifolia* invading the St. Lucia estuary in KwaZulu-Natal, South Africa (photograph: LJ Potgieter)

following the methodology of Procheş (2006) and Procheş et al. (2012) using ESRI ArcView v.10.0 (Fig. 3). Occurrence records for each species from several databases, namely the Invasive Species Compendium (CAB International 2000, http://www.cabi.org/ISC/), Global Biodiversity Information Facility (GBIF 2008, http://www.gbif.org) and Atlas of Living Australia (www.ala.org.au/), were used to map the native, introduced and naturalized ranges of each species.

Casuarinas are now found across most tropical and sub-tropical regions, with many species in China, India, Kenya, Senegal and Tanzania (Fig. 3b). Despite the paucity of published sources for most parts of Africa, various unpublished sources and anecdotal evidence indicates that the genus has been widely disseminated throughout the continent. Introductions have resulted in the naturalization and invasion (sensu Pyšek et al. 2004) of three species in many parts of the world (Fig. 3c).

The potential global distribution of casuarinas

A close match between broad-scale climate in the native and receiving ranges is an important requirement for

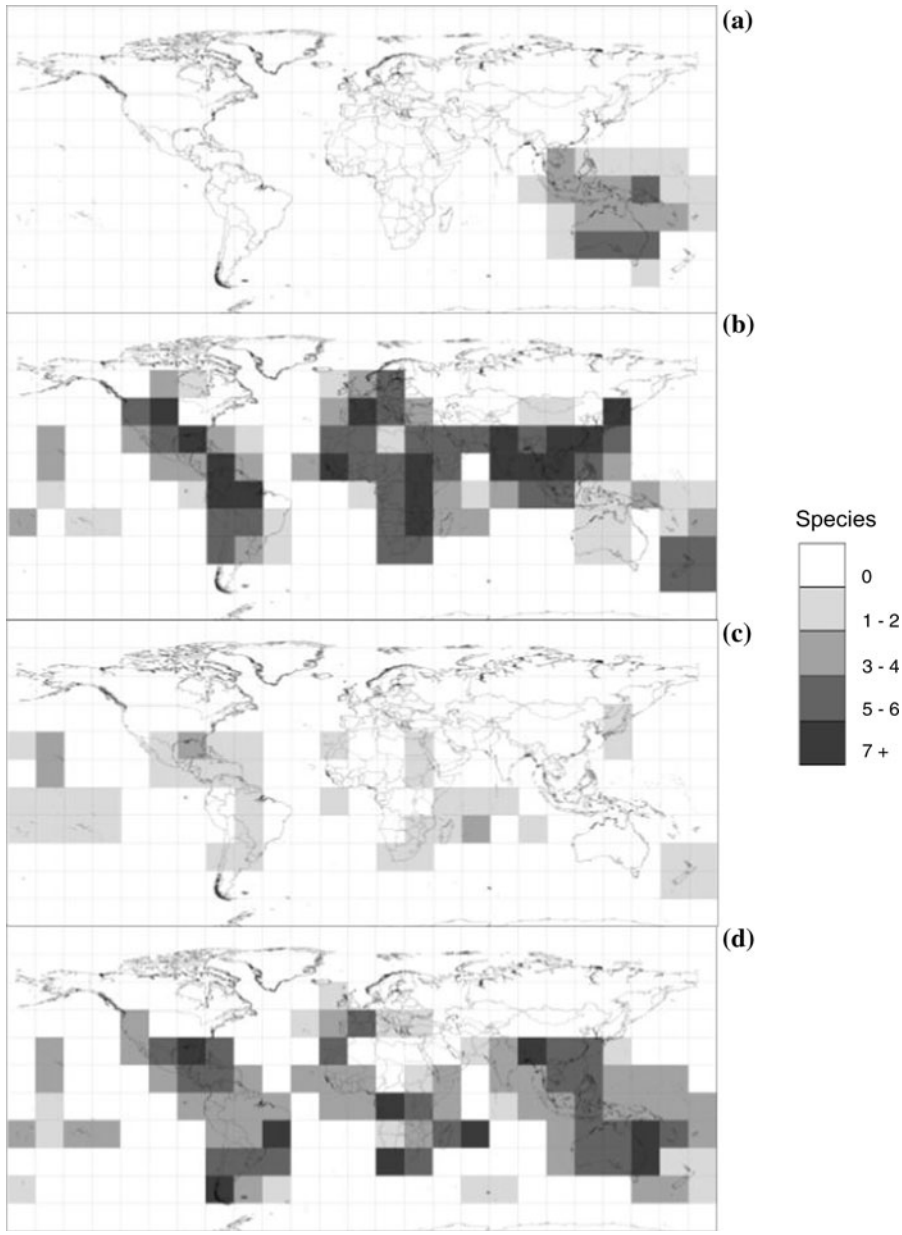

Fig. 3 The global diversity of *Casuarina* species: **a** native distribution; **b** introduced distribution; **c** naturalized distribution; **d** potential range based on climatic suitability. Data from Australia's Virtual Herbarium, Global Biodiversity Information Facility, Atlas of Living Australia and Invasive Species Compendium. The potential species richness map was obtained by combining results of bioclimatic species distribution models created for each taxon

naturalization and invasion of alien plants (Richardson and Pyšek 2012). Species with large climatic or geographical native ranges are more likely to become invasive elsewhere (van Kleunen et al. 2011). To derive a rough estimate of climatic suitability and therefore the potential global range of casuarinas, we built bioclimatic models for each species using MaxEnt v3.3.3 (Phillips et al. 2006; Fig. 3d; Appendix S2 in Electronic Supplementary Material). We compiled occurrence records from Australia's Virtual Herbarium (avh.ala.org.au/). Nine interpolated bioclimatic variables (2.5 min spatial resolution) were obtained from WorldClim (http://www.worldclim.org, Hijmans et al. 2005) and used as predictor variables for developing simple climate envelope models for each species. The climatic variables used were: annual mean temperature, isothermality, temperature seasonality, maximum temperature of warmest month, temperature annual range, mean temperature of wettest quarter, annual precipitation, and precipitation of warmest quarter. A random 75 % of the presence points

were used to develop each model; the remaining 25 % were used to test model performance. The final model was chosen using the highest AUC (area under the receiver operating curve; Elith et al. 2006). We used the lowest presence threshold (Pearson et al. 2007) to define climatically suitable areas. Climatic suitability maps for each species were generated in ArcMap where each grid cell had values ranging continuously from 0 (low suitability) to 1 (high suitability). These values can be interpreted as the probability of presence of suitable environmental conditions for the target species. The symbology was altered to achieve an appropriate colour representation. The dark areas indicate suitable habitat and the lighter areas represent unsuitable or marginal habitat. The same measured grid of 15 × 15 decimal degrees used for the distribution mapping was overlaid on the map at the same geographic coordinate system. A final map of species richness was compiled indicating the potential species richness in each 15° × 15° square. A contingency table was constructed in which naturalization and climate suitability were correlated using the number of countries in which *C. cunninghamiana*, *C. equisetifolia* and/or *C. glauca* have been introduced (Table 2). A Chi square test was used to determine whether climatic suitability is significantly correlated to naturalization.

Roughly 8 % of the earth's land area is bioclimatically similar to the native ranges of casuarinas (Fig. 3d). *Casuarina* species have been introduced to most parts of the world identified as being climatically suitable. In the introduced range, Central and South America, Southeast and southern Africa, the Caribbean and Southeast Asia are regions of high climatic suitability (Fig. 3d). Climate suitability does provide some predictive information of naturalization ($\chi^2 = 8.78, p < 0.05$; Table 2).

It is unsurprising that some of the major areas of *Casuarina* invasions, namely Florida and La Réunion Island (see Boxes 1, 2), are predicted to be climatically suitable for *C. cunninghamiana, C. equisetifolia* and *C. glauca* (Fig. 3c; Appendix S2 in Electronic Supplementary Material), though these areas are also climatically suitable for an additional four species not yet introduced as far as we know (Fig. 3d). South Africa is climatically similar to Australia (Richardson and Thuiller 2007)—the native range of many *Casuarina* species. Five species have been introduced into South Africa in the past (Poynton 1995) and two species are currently naturalized: *C. cunninghamiana* and *C. equisetifolia* (Henderson 2007). Appendix S2 in Electronic Supplementary Material shows that coastal areas of South Africa are suitable for *C. cunninghamiana*, *C. glauca* and to a lesser extent *C. equisetifolia*. South Africa is also suitable for two other introduced species: *C. cristata* and *C. junghuhniana* (Fig. 3d). Given the climatic suitability of South Africa for the above-mentioned species, we can expect further naturalizations in the future. Large plantations of several *Casuarina* species have been established in southern China, India and Taiwan—regions which are climatically suitable for at least six *Casuarina* species (Fig. 3d) including the three invasive species (Appendix S2 in Electronic Supplementary Material). Apart from a few unpublished reports on casuarinas becoming problematic on the Indian coast, it is surprising that few records of naturalization in these countries exist. In Hawaii, *C. cunninghamiana*, *C. equisetifolia* and *C. glauca* are classified as invasive, but Appendix S2 in Electronic Supplementary Material shows that the island group is only climatically suitable for one invasive species. Large parts of Argentina, Brazil and Southeast Africa are climatically suitable for all three invasive species and

Table 2 The link between climatic suitability and naturalization in *Casuarina*. Contingency table of 97 instances where *C. cunninghamiana*, *C. equisetifolia* and/or *C. glauca* have been introduced to a country. Naturalization was recorded in 36 countries, only 4 of which were in climatically unsuitable areas (i.e. model errors). In another 61 cases, no naturalization is recorded. *Casuarina cunninghamiana*, *C. equisetifolia* and/or *C. glauca* have been introduced to 37 climatically suitable countries where they have not yet become naturalized—suggesting a substantial invasion debt. Climatic suitability was determined based on the model where the lowest presence threshold (Pearson et al. 2007) was used to define climatically suitable areas on a continuous scale of 0 to1 (0 = low suitability and 1 = high suitability). Naturalization (sensu Pyšek et al. 2004) in each country was determined by evidence in the literature. Y yes and N no. Chi square = 8.78; $p < 0.05$

Climatically suitable	Naturalized	
	Y	N
Y	32 Correctly predicted naturalizations	37 Potential invasion debt
N	4 Model errors	24 Plantations in areas unsuitable for naturalization

Box 1 *Casuarina* in Florida, USA

This case study provides useful insights on the rationale behind introductions of *Casuarina* species, their impacts, changing views of the benefits and costs of casuarinas, and the evolution of management strategies.

Introduction history and uses

Seeds of four *Casuarina* species (*C. cristata*, *C. cunninghamiana*, *C. equisetifolia* and *C. glauca*) were introduced to the USA from France in 1898. These species were planted along beaches and near homes for protection against hurricanes and strong winds (Schmid et al. 2008). Seeds were often distributed under erroneous names and misidentification is still a problem (Morton 1980). Casuarinas were initially used for forestry, but the arrival of bacterial canker (spread by wind-blown rain) on citrus in 1995 led to an increase in their use as windbreaks (Fig. 1f). *Casuarina cunninghamiana* was most widely used for this purpose based on its successful use for this purpose elsewhere in the world and its apparent non-invasiveness (Castle et al. 2008).

Impacts

Casuarina cunninghamiana, *C. equisetifolia* and *C. glauca* and are currently considered among the most severe invaders in Florida (Wheeler et al. 2011). These three species and their hybrids aggressively invade inland (Fig. 2a, f) and coastal habitats and threaten biodiversity and beach integrity (Morton 1980). *Casuarina equisetifolia* and *C. glauca* have transformed beach, dune, and coastal scrub communities into closed-canopy forests with little understorey (Gordon 1998). *Casuarina equisetifolia* has had a range of effects in invaded ecosystems, including increased erosion rates resulting from exclusion of native soil stabilizers (Crooks 2002). This species out-competes native plants and replaces entire natural plant communities (Brock et al. 1997). High rates of litter fall from *C. equisetifolia* can potentially suppress the recruitment of other species (Gordon 1998). Nesting of loggerhead sea turtles is physically impeded by fallen trees and the formation of steep shorelines (Office of Technology Assessment 1993). Rodent densities and understorey growth are reduced (Crooks 2002). Casuarinas also pose a threat to human health as the seasonal release of pollen results in respiratory ailments (Morton 1980). During hurricanes, fallen branches and/or trees (up to 30 m) directly damage homes, power lines, power poles, and block evacuation roads. In northern areas of the state, frost-killed trees become problematic due to the fall of branches and crowns.

Management

The Florida Exotic Pest Plant Council (FLEPPC) (2010) defined these three species as ''invasive exotics that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with natives''. *Casuarina equisetifolia* and *C. glauca* are classified as Category 1 invaders, and *C. cunninghamiana* as a Category 2 invader (FLEPPC Plant List Committee 2010). They are prohibited under state environmental policies and cannot be held, collected, transported, cultivated, or imported without a permit from the Department of Agriculture and Consumer Services. This Department is currently developing and implementing a monitoring protocol to determine the invasiveness of *C. cunninghamiana.*

A hurricane in 1986 caused extensive damage due to wind-blown casuarinas on Sanibel Island off Florida coast and triggered management action. Efforts to remove all casuarinas from this area (state-owned and private land) and re-vegetate with native plants are underway.

No specific management plans are being implemented for casuarinas elsewhere in Florida, but guidelines have been proposed for their control (Langeland et al. 2011). Recommended herbicide treatments are: Basal bark application: 10–20 % Garlon 4; Cut stump: 50 % Garlon 3A or 10–20 % Garlon 4 (remove scaly bark if present); Frill (larger trees): 20 % Garlon 4. The addition of 3 % Stalker will increase consistency on older trees; soil: 4–6 pounds Velpar ULW/acre.

The Australian Biological Control Laboratory in Brisbane, Australia, in collaboration with the US Department of Agriculture, are investigating host range and host specificity of potential insect herbivores for the biological control of casuarinas (CSIRO 2011). A number of insects have been identified as potential agents. Priority is being given to foliage- and seed-feeding insects such as gall-forming wasps, defoliating moths and seed feeders (CSIRO 2011). Genetic studies are being conducted to determine the variation in *Casuarina* species in Australia and Florida to locate the source populations of the weed in the introduced range (CSIRO 2011). Research into the evolutionary associations between *Casuarina* and its associated herbivores is also planned (CSIRO 2011).

given that these species have been introduced to these areas, naturalizations and invasions can be expected in the future. Four countries (Egypt, Japan, Iraq and Israel) in which casuarinas are naturalized, fell outside areas identified as being climatically suitable (Table 2). The performance of *C. junghuhniana* needs to be monitored in countries such as Kenya, Tanzania, Senegal, Uganda, China, India, Taiwan and Thailand where large-scale plantings have been established in climates similar to its native range. Other taxa which, although not yet widely planted, could invade certain habitats include *C. cristata* (Doran and Turnbull 1997) and *C. obesa*. The lack of reports of naturalization is some instances could be due to short residence times. The majority of records of *Casuarina* naturalization and invasion come from areas where both the climatic conditions are suitable and casuarinas have been planted for more than 50 years.

Box 2 *Casuarina* in the Mascarene Islands

Casuarinas are now emblematic of the Mascarene Islands, an archipelago in the southern Indian Ocean east of Madagascar comprising Mauritius, La Réunion and Rodrigues. Many shops, hotels, restaurants are named 'filao'—the local name for casuarinas. This case study provides insights into the varying levels of success achieved by casuarinas, and reveals how different perceptions and management efforts have developed on different islands.

La Réunion Island

The native flora of Réunion Island is threatened by many invasive woody plants introduced for agriculture, forestry or as ornamentals (Tassin et al. 2006a). Among these are *Casuarina cunninghamiana* (introduced in 1840), *C. equisetifolia* (introduced in 1768) and *C. glauca* (introduced in 1877) (Baret et al. 2006). These species were mainly used for firewood, but also for erosion control (Kueffer and Vos 2004). By the early 1900s, all fuel-wood used in the lowlands came from *Casuarina* plantations around the coast (Cheke and Hume 2008). By the 1920s, over a million *Casuarina* trees had been planted on the island (Cheke and Hume 2008). After World War II, the Forest Service began large-scale planting to replace natural forest with alien trees, mainly species of species of *Acacia*, *Casuarina* and *Cryptomeria* (Kueffer and Lavergne 2004). Low-altitude habitats were greatly reduced, transformed and fragmented by the combination of human activities (agriculture, urbanization) and invasion by introduced species (Strasberg 1996). Currently, large-scale disturbances such as lava flows, fire and hurricanes may facilitate *C. equisetifolia* invasions on the island. *Casuarina equisetifolia* has increased substantially in abundance and distribution since Macdonald et al.'s (1991) ranking of invasive plant species (Baret et al. 2006). *Casuarina cunninghamiana* invades inland slopes at higher altitudes (Baret et al. 2006) while *C. glauca*, which is not mentioned by Macdonald et al. (1991), also invades upland areas of the island (Tassin et al. 2006b).

Impacts

Casuarina equisetifolia is a major transformer species on La Réunion and invades volcanic lava flows (Fig. 2d) and coastal regions where it forms dense monospecific stands, affects nutrient cycling (Kueffer and Lavergne 2004), and interferes with early natural succession (Macdonald et al. 1991). The impacts of *C. cunninghamiana* and *C. glauca* on the island have not yet been assessed.

Management

In 2007 the Forest Service initiated a control programme for *C. equisetifolia* along the south-eastern coast (supralittoral zone) with the aim of restoring coastal habitat. At local scales, results have been promising, and native species have started to re-emerged. No management attempts have been made for *C. cunninghamiana* and *C. glauca.* The forestry sector is currently shifting emphasis from production forestry to nature conservation and invasive species control. A national invasive species committee has been set up and on-going research projects attempt to assess the impacts of control methods. Problem species and areas have been prioritised for control. Options for biological control of casuarinas have not yet been assessed.

Mauritius

Increased agriculture, the emancipation of slaves, the demand for wood for the railways, and the introduction of alien plant species during the eighteenth century contributed to the degradation of the native forest (Kueffer and Mauremootoo 2004). The first seedlings of *C. equisetifolia* were brought to the island in 1778, and British colonialists distributed seedlings all over the island (Cheke and Hume 2008). Large-scale reforestation started in the late nineteenth century and continued until the mid-1970s (Kueffer and Mauremootoo 2004). Casuarinas were planted along the coastline as part of a tree and water conservation programme and to protect against beach erosion and sea gusts (Cheke and Hume 2008). *Casuarina equisetifolia* is now naturalized (Sandlund et al. 2001) and has begun to spread in certain areas (e.g. on Ile aux Benitiers) off the southwest coast where plantations have reached maturity and regenerate spontaneously and on Le Morne Mt. where individuals are spreading up the mountain flank from a plantation (Cheke and Hume 2008). A plantation of another *Casuarina* species (yet to be identified) has been established inland near the Cabinet Nature Reserve, but no spread has been observed (Cheke and Hume 2008).

Impacts

Impacts for casuarinas on Mauritius have yet to be assessed

Management

The island is still in the phase of planting *C. equisetifolia* rather than controlling it. There have, however, been recommendations to remove the species from coastal areas and to replace it with a more native tree mix for shade and erosion control.

Rodrigues Island

The human population on this small island (109 km^2) grew from 100 to 35,000 between 1800 and 1950. In 1845, most of the natural forest had been removed through tree felling, wood burning, browsing (by goats), trampling (by cattle), rooting (by pigs), and overgrazing. It was then suggested that the island could support more than 12,000 cattle if a "few improvements" were done (Cheke and Hume 2008). Among these "improvements" was the planting of *C. equisetifolia* in the uplands; the species was introduced in 1876. In the early 1900s, the planting of casuarinas was again recommended in coastal areas and on light soils to provide shade and improve grass cover. "Agricultural improvements" commenced again in 1955, when large areas of natural forest were cut and replanted with alien trees such as casuarinas for timber production and watershed protection (Cheke

Box 2 continued

and Hume 2008). While casuarinas produced firewood, they did not provide food or shelter to endemic wildlife or supply sufficient shade for effective cover on dry slopes. They are used for hedges, fences, windbreaks, fuel-wood, and timber for fishing boats and house construction (Muenier 1990). *Casuarina equisetifolia* is now naturalized (Sandlund et al. 2001).

Impacts

The impacts of *C. equisetifolia* on Rodrigues Island have yet to be assessed.

Management

A pilot coastal restoration project funded by European Union from 2002–2003 was implemented to restore native vegetation in two contrasting coastal plots (areas planted with *C. equisetifolia*). This project aims to establish workable methodologies for future coastal restoration through experimentation.

Ecological and economic importance of *Casuarina* and the rationale for introductions

Invasion pathways for woody invasive species are shaped by the demand for the species in the receiving environment (Richardson and Rejmánek 2011). Trees are often cultivated in large numbers, at multiple foci and close to many potentially invasive habitats (Richardson 1998). Cultivated trees are nurtured and protected from disturbance effects, allowing them to attain maturity and accumulate large propagule banks.

The global demand for fast-growing trees increased sharply from the middle of the nineteenth century when many species were tested and transported around the world (Bennett 2011), e.g. as part of the Empire Forestry movement (Barton 2002). Australian tree species of the genera *Acacia*, *Casuarina* and *Eucalyptus* were well suited to warmer climates and proved to be of substantial economic value (Bennett 2010), and are now prominent features in many landscapes around the world. The selection of a particular species depends on several factors: the climatic conditions in the area, proximity to the sea, wind, soil erosion and soil mineral deficiencies at the plantation sites (Sayed 2011). At least six *Casuarina* species have been widely introduced and extensively cultivated (Wilson and Johnson 1989; Steane et al. 2003). Historically, casuarinas were planted on relatively poor soils as they grew well where most other tree species did not. They were generally not considered high-value trees, but filled an important ecological niche.

The number of uses for casuarinas continues to increase. Casuarinas, along with acacias and eucalypts, are key taxa where major reforestation programmes are underway or are being considered in many parts of the world. The wood of casuarinas is an important source of firewood and charcoal (Fig. 1d) and is often used for general construction purposes (poles, fences, rafters, beams, tool handles etc.) (Fig. 1h, l) and other wood-based industries (veneer for plyboard and woodchips for paper pulp) (Zhong et al. 2010a). Casuarinas are commonly planted for windbreaks (Poynton 1995; Castle 2008) (Fig. 1f) and erosion control, particularly along coastlines, sand dunes and river banks (Parrotta 1993). Forbes and Broadhead (2007) and Zhong et al. (2010b) stress the importance of *C. equisetifolia* as shelter trees during typhoons and tsunamis in Asia. In India, vast plantations of *C. equisetifolia* (funded and facilitated by various non-government and international organisations like the World Bank) have been established along the coast to act as bioshields. They are grown as ornamental (Fig. 1c) and shade trees (Fig. 1b) and are often pruned into hedges (Parrotta 1993). They are widely used in agroforestry and for rehabilitation (Fig. 1a) and wood production programs (Zhong et al. 2010a). They enhance ecosystem fertility (Diagne et al. 2013) and are therefore valued as pioneer trees for intercropping (Fig. 1g), soil improvement and degraded sites due to their N-fixing capabilities and high rates of litter production (Zhong et al. 2010a). The bark of casuarinas is rich in tannin and is used for dyeing leather and fishing nets (Parrotta 1993). The bark and branchlets may have medicinal properties and are used to treat beriberi by some native communities in New Zealand (Parrotta 1993). Although of limited value as a source of fodder, casuarinas are sometimes used for this purpose during times of drought (Doran and Hall 1983).

Casuarinas as naturalized and invasive alien trees around the world

A number of mechanisms may explain some of the variation in performance of the same invasive species

across multiple introductions (Kueffer et al. 2010, 2013). A better understanding of these factors will improve our ability to predict the outcome of *Casuarina* introductions.

Despite the large and growing distribution of the genus outside its native range, very little is known about the invasion ecology of casuarinas. We know of no detailed studies of the invasion ecology of any *Casuarina* species at any site (this is in marked contrast to acacias, eucalypts and pines where invasions have been studied at many sites). *Casuarina* species invade habitats of strongly contrasting characteristics (e.g. beach crests, young volcanic flows, riparian ecosystems) where the requirements for successful invasion are quite different to other tree taxa. In their global review of invasive trees and shrubs around the world, Rejmánek and Richardson (2013) present evidence of three *Casuarina* species being invasive in nine regions around the world. *Casuarina equisetifolia* was noted as being invasive in North America (Florida) (Fig. 2f), Asia, Southern Africa (Fig. 2i), Central America, South America. *Casuarina equisetifolia* is considered invasive on the following islands: Ascension, Bermuda, Canary Islands, Cayman Islands (Fig. 2h), Dominican Republic, Hawaii, Jamaica, La Réunion (Fig. 2d), Ogasawara, Puerto Rico, Seychelles (cf. Kueffer et al. 2010). *Casuarina cunninghamiana* was noted as invasive in southern Africa and La Réunion Island (Box 2). *Casuarina glauca* was listed as invasive in North America (Florida) and the Pacific Islands (Hawaii) (Figs. 2b, c, g), and recorded as a potential invader in Madagascar. *Casuarina equisetifolia* is the most widely planted species in the genus and also the most invasive.

We use different case studies from key *Casuarina* invasions around the world (see Boxes 1, 2). These case studies serve as a tool for facilitating the development of screening models for given systems by providing useful insights into the rationale behind human-mediated introductions, impacts on different ecosystems and management approaches adopted in different parts of the world for a globally important group of plants. In these case studies, casuarinas were introduced into different environments, at different times, for different purposes where various human and environmental disturbances have facilitated establishment. Perceptions of casuarinas, stages in the introduction-naturalisation-invasion continuum, the impacts associated with invasion, and management efforts differ markedly in each region. Comparable conflicts of interest exist in each region as the benefits of casuarinas are weighted against the costs.

The expanding global range of *Casuarina*

As with Australian acacias (Richardson et al. 2011), not all *Casuarina* species have been moved out their native ranges to the same extent over the same periods, and some have not been moved at all. This complicates the task of separating human factors from biological mechanisms as mediators of invasion success. In this section we quantify the importance of casuarinas around the world and explore the link between native range size and naturalized success.

The importance of casuarinas globally

To derive a rough measure of the relative importance of *Casuarina* species in different parts of the world, we ran a search for "casuarina" in the CAB Abstracts Database for the period 1966–2012 (3 August 2012; http://www.cabi.org/) (CAB International, Wallingford, Oxford, UK). The CAB Abstracts Database has been shown to be a useful source of information for deriving a rough measure of the global distribution of tree species with commercial value, e.g. for *Pinus* (Richardson et al. 1994; Procheş et al. 2012). Each abstract was manually searched and the location for each species recorded. The *Casuarina* species in Appendix S3 in Electronic Supplementary Material are those that have been introduced around the world and propagated to various degrees by humans. Some (but not all) species are commercially important. For a more detailed dataset, see Appendix S4 in Electronic Supplementary Material.

Figure 4 shows the number of countries into which casuarinas were introduced at various times. Eight species (and one hybrid) in the genus have been widely introduced around the world and three have become naturalized/invasive in many countries. These three species are the most widely introduced, and *C. cunninghamiana* has experienced the greatest introduction effort. Most introductions took place between 1950 and 2000—too recently for widespread invasions to have been reported. This points to a substantial invasion debt.

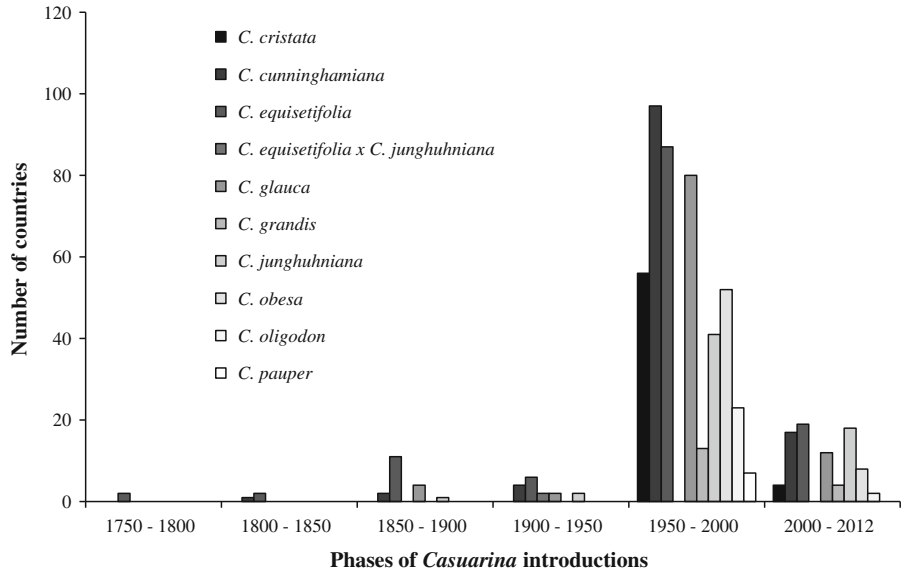

Fig. 4 The number of countries in which *Casuarina* species were first introduced during the respective time frame. Note that the last time frame is only 12 years. Most documented introductions of casuarinas occurred during the second half of the twentieth century. Data from the Australian Tree Seed Centre

The relationship between the native range and the naturalized success

A positive relationship between the size of the native range and the likelihood of becoming invasive has been demonstrated for many plant taxa, including Australian tree taxa (Hui et al. 2011). In addition, tolerance of a wide range of climates in the region of origin is an important determinant of invasiveness for a species (Pyšek et al. 2009b). Several studies have also shown a strong positive relationship between the extent of human usage and the adventive range of alien plants (Wilson et al. 2007; Castro-Díez et al. 2011). We were interested to determine the relationship between native range size for *Casuarina* species and the extent of introductions around the world, naturalized range size and extent of invasiveness.

We tested the relationship between native and naturalized range sizes using a Spearman's rank correlation for all species (Fig. 5a). *Casuarina equisetifolia*, *C. cunninghamiana* and *C. glauca* are naturalized in 32, 13 and 6 countries respectively (36 countries in total). There is a positive correlation between native and naturalized range sizes ($r = 0.84$; $p < 0.005$). A large native range size is strongly associated with naturalization (Fig. 5a). While this is in line with the link between invasiveness and range size, it is not clear what the mechanisms are. However, human interest in a given taxon may explain much of the variation in the extent of naturalization (Appendix S3 in Electronic Supplementary Material). This is in agreement with other recent studies (Pyšek et al. 2009a; Procheş et al. 2012).

We plotted the frequency of citations in the forestry literature (as a crude proxy for planting intensity; see above) against native range size and naturalized range size (Fig. 5b) of all *Casuarina* species. Note that a strong bias exists in favour of data for developed countries. Naturalized species tend to have greater coverage in the literature (Fig. 5b) than species that have not become naturalized. Of those that are naturalized, those with more citations in forestry abstracts in the CAB Forestry Compendium tended to have larger naturalized ranges (Fig. 5b). There were no citations for *C. orophila*, *C. potamophila*, *C. tenella* and *C. teres.*

Do certain life-history traits make some *Casuarina* taxa more invasive?

Understanding whether successful invaders possess a distinct set of life-history traits is important for the prediction and management of future invaders

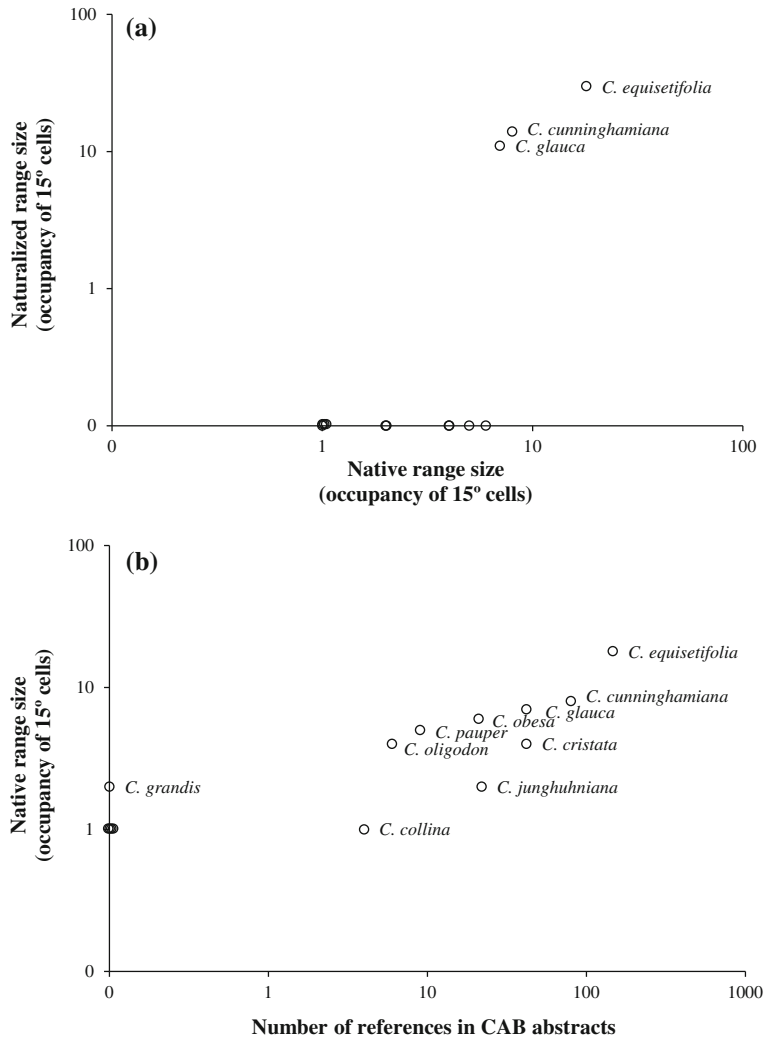

Fig. 5 The relationship between **a** native and naturalized range sizes and **b** number of references in the forestry literature and native range size in *Casuarina* species (number of 15° squares occupied; symbols jittered to show multiple species with identical values)

(Hamilton et al. 2005). We explore whether certain life-history traits (Table 3) predispose some casuarinas to become naturalized in their new ranges.

Human-mediated dissemination of important species to and within new regions increases the risk of invasion (Castro-Díez et al. 2011). Traits associated with the ecological performance of a species (and consequently potential invasiveness) in new environments are closely related to traits associated with human use (Castro-Díez et al. 2011; Richardson et al. 2011). This complicates attempts to explain the extent of naturalization/invasion of introduced species, since patterns of invasion may simply reflect levels of introduction effort and propagule pressure which may mask potentially important roles of other factors. High levels of propagule pressure as a result of planting, inevitably lead to the escape of woody species from cultivation, irrespective of biological traits (Pyšek et al. 2009a).

As is the case with Australian acacias (Richardson et al. 2011), accurate data on most traits is only available for a sample of *Casuarina* species—generally only those species that are most useful to humans. Consequently, correlating performance as introduced species with traits across the full spectrum of species is difficult. The same traits that allow a species to be widespread in the native range should contribute to their ability to overcome abiotic filters and successfully establish in a new region (Schlaepfer et al. 2010). Differences in a few key traits between closely-related species can promote invasiveness (Funk et al. 2008).

Table 3 Selected life-history traits and environmental preferences for *Casuarina* species

Casuarina species	Breeding system	Max. tree height (m)	Samara length (mm)	Seed size (mean number of seeds kg^{-1})	Coppicing ability	Propagation	Nodulation	Status as introduced taxa (sensu Pyšek et al. 2004)	Tolerance of abiotic factors	Factors potentially limiting naturalization/invasion
C. collina	Dioecious[5]	15–20[5]	?	?	?	Root Suckering[5], seed[5]	Present[5]	Alien	Fire resistant[5], infertile soil[5]	?
C. cristata	Dioecious[12]	10–20[2]	3–4[2]	111,900[11]	Yes[2]	Root Suckering[12], seed[2]	Minimal[2]	Alien	Drought[12], moderately saline soils[2], waterlogging[2], frost[2]	Seedlings and suckers grazed by livestock[12]
C. cunninghamiana	Dioecious[12]	12–35[11]	3–4[11]	607,200[11]	Yes[11]	Root Suckering[12], seed[15]	Prolific[12]	Invasive	Cold temperatures[12], drought, moderate soil salinity[15], frost[15], wind[15]	Seedlings susceptible to browsing[12], fire-sensitive[11]
C. equisetifolia	Monoecious[12]	6–35[11]	4–5[15]	268,200[11]	Yes[12]	Seed and/or vegetative[15]	Prolific[12]	Invasive	Infertile soil[12], drought[15], coastal salt spray[15], high soil salinity[15], waterlogging[15], wind[15]	Browse-[12], fire-[12], frost-[12], and shade-sensitive[12], cold temperatures[12], seedlings susceptible to disease[12], susceptible to root rot[12]
C. glauca	Dioecious[12]	8–20[11]	3.5–5[11]	414,900[11]	Yes[12]	Root suckering[12], seed[12]	Prolific[12]	Invasive	Coastal salt spray[12], waterlogging[12], drought[12], highly saline, acidic and alkaline soil[12]	Suckers grazed by livestock[12], frost-sensitive[12]
C. grandis	Dioecious[8]	35–40[8]	?	?	?	Root suckering[8], seed[8]	Present[13]	Alien	?	?
C. junghuhniana	Dioecious[12]	15–25[11]	4–5[11]	1,000,000–1,800,000[11]	Yes[12]	Root suckering[12], seed and/or vegetative[16]	Minimal[12]	Alien	Drought[12], waterlogging[11]	Hybrid trees do not produce seeds[7,12]
C. obesa	Dioecious[12]	3–15[10]	5–7[10]	840,000[12]	No[4]	Root suckering[12], seed[1]	Prolific[12]	Alien	Drought[4], high soil salinity[10], waterlogging[10], frost[10], wind[10]	Suckers grazed by livestock[4]
C. oligodon	Dioecious[12]	30[11]	4[11]	1,500,000–2,000,000[11]	Yes[11]	Seed[11], epicormic shoots[12]	Present[12]	Alien	High humidity[12]	Sensitive to saline soils[12], susceptible to wind damage[12]
C. orophila	?	?	?	?	?	?	Present[13]	?	?	?

Table 3 continued

Casuarina species	Breeding system	Max. tree height (m)	Samara length (mm)	Seed size (mean number of seeds kg^{-1})	Coppicing ability	Propagation	Nodulation	Status as introduced taxa (sensu Pyšek et al. 2004)	Tolerance of abiotic factors	Factors potentially limiting naturalization/invasion
C. pauper	Dioecious[14]	6–15[14]	?	?	?	Seed[14]	?	?	Moderate soil salinity[14], waterlogging[14]	?
C. potamophila	?	?	?	?	?	?	?	?	?	?
C. tenella	?	?	?	?	?	?	?	?	?	?
C. teres	?	?	?	?	?	?	?	?	?	?

[1] Blake (2009); [2] Doran and Turnbull (1997); [3] Elfers (1988); [4] Emmott and Greening Western Australia (2001); [5] Gauthier et al. (1999); [6] Halliday (1984); [7] Jayaraj (2010); [8] Johnson (1982); [9] Marcar and Crawford (1995); [10] NSW Government (2012); [11] Orwa et al. (2009); [12] U.S. National Research Council (1984); [13] Varma (2008); [14] Victorian Resources Online (2011); [15] Whistler and Elevitch (2006); [16] Zhong et al. (2010a)

Casuarinas possess a range of traits that make them popular as multipurpose trees, but the same traits also enhance their invasive capacity and their ability to cause impacts in invaded ecosystems. Such traits include: rapid growth; a tolerance of high salinity, cold temperatures, low soil fertility and arid conditions; the capacity to establish and propagate easily; the ability to coppice; and the production of dense wood (Table 3). Symbiotic associations with N-fixing actinobacteria from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi allow them to grow in and enrich degraded and waste land soil (Diagne et al. 2013). Their enormous reproductive capacity, ability to rapidly colonize disturbed/open habitats, short juvenile period, and their ability to grow well at high densities make them useful for many purposes (Rockwood and Geary 1991) but also contribute to their weediness.

Rejmánek and Richardson (2006) showed that life-history traits clearly separate invasive from non-invasive *Pinus* species. However, no life-history traits (or suite of traits) clearly separate invasive from non-invasive *Casuarina* species (Table 3). Native range size and the level of dissemination and propagule pressure resulting from human usage seem to be much better predictors of invasiveness and invasion success of casuarinas than any single trait or combination of traits.

Ecological factors that potentially influence the invasion ecology of casuarinas

Key traits and/or trait combinations of economically and ecologically important tree species are associated with their roles as early-seral plants (Strauss and Ledig 1985) and potential invaders (Richardson 1989). Here, we discuss some important ecological factors that contribute to the invasive success of casuarinas. Most of these factors have not been studied in the context of invasion ecology and further work is needed.

Symbiotic associations

Alien plant and microbe mutualists can facilitate each other's spread as they co-invade new ranges (Porter et al. 2011). Casuarinas form symbiotic N-fixing associations with soil actinomycetes from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi (Zhong et al. 1995; Wang and Qiu 2006). These symbiotic associations allow casuarinas

to fix nitrogen at rates similar to nodulated legumes (Zhong 1993). As for Australian acacias (Morris et al. 2011), N-fixation can result in alteration of soil-nutrient cycling and enrichment of soil N which hinders the competitive ability of native species. N-fixing species have been shown to severely alter ecosystem function (Vitousek and Walker 1989). This may relate to the empty niche hypothesis as N-fixing species may be particularly problematic on islands as they fill an empty niche (Vitousek and Walker 1989).

The association of *Casuarina* roots with both types of mycorrhizae significantly enhances the adaptability of these species and their ability to grow in harsh environments. Specifically, the fungi help the trees by: improving mineral nutrition (increasing availability of phosphorus and increase absorption of soil nitrogen) (Elumalai and Raaman 2009; Zhong et al. 2010a, b); increasing tolerance to drought (Zhang et al. 2010), flooding (Osundina 1997) and salt stress (Evelin et al. 2009); influencing the N-fixing ability of *Frankia* (He and Critchley 2008); improving soil structure (hyphal mats contribute to soil binding); increase disease resistance (by preventing access of the pathogen to the plant root) (Liu et al. 2007; Akhtar and Siddiqui 2008); and alleviating the effects of acid soils (Diem et al. 2000). *Casuarina* roots also interact with unidentified soil microorganisms that cause the development of proteid roots (Diem et al. 2000). These roots appear to greatly increase the surface area for nutrient absorption, however little is known about their benefits. These associations help casuarinas to occupy nitrogen-poor sites such as coastal dunes and disturbed areas. A study in Senegal showed that the amount of soil nitrogen under *Casuarina* trees increased by 58 kg ha^{-1} $year^{-1}$ when compared to nearby sand dunes without casuarinas (U.S. National Research Council 1984). This partly explains the popularity of casuarinas for dune stabilization, land reclamation, intercropping and agroforestry (Zhong et al. 1995). The rate of N-fixation is species-dependant and also differs according to environmental factors and the strain of the *Frankia* symbiont (U.S. National Research Council 1984). While certain *Casuarina* species may combine mycorrhizae and N-fixing nodules in some areas, these mutualisms may be mutually exclusive in others (Orians and Milewski 2007). Richardson et al. (2000) suggested that co-invasion by specific strains of *Frankia* is critical to the success of casuarinas, but this has not been verified.

Hybridization

Hybridisation in plants allows for an increase in genetic variation and production of novel gene combinations, potentially fuelling the evolution of invasiveness (Gaskin et al. 2009). Interspecific hybridization, which may contribute to the success of invasive species (Ellstrand and Schierenbeck 2000), occurs among casuarinas (Wheeler et al. 2011) making species' identification difficult (Ho et al. 2002). *Casuarina equisetifolia* is monoecious and is therefore well adapted to propagate itself as individual plants easily self-seed (Castle et al. 2008). Thus, the likelihood of interspecific hybridization is significantly higher when in close contact with other species (Castle et al. 2008). *Casuarina glauca* and *C. cunninghamiana* are dioecious suggesting that male and female plants would need to be in close proximity to one another in order to produce hybrid seeds (Castle et al. 2008). Gaskin et al. (2009) reported hybrids between *C. equisetifolia* and *C. glauca* and possibly between *C. glauca* and *C. cunninghamiana* in Florida. Even though the native ranges of these species overlap, Gaskin et al. (2009) detected no hybridization in Australia. In Egypt, several hybrids (e.g. the natural hybrid *C. cunninghamiana* × *C. glauca*) have been selected for improved biomass production under a range of environmental conditions (El-Lakany 1996). Ho et al. (2002) and Ho and Lee (2011) suggest that cultivated casuarinas in Taiwan are the result of introgressive hybridization involving *C. equisetifolia*, *C. glauca*, and possibly *C. cunninghamiana*. Their results also imply that most casuarinas in Taiwan are derived from the backcrossing to *C. equisetifolia*. In addition, Ndoye et al. (2011) suggested that cultivated populations of *C. equisetifolia* in Senegal are subject to hybridization and inbreeding depression. Chen and Li (2002) showed that very high inbreeding retrogression occurred in a *C. equisetifolia* plantation on the southeast coast of the People's Republic of China, indicating that inbreeding and its subsequent retrogression played an important role in the decline of the plantation. A hybrid of *C. junghuhniana* and *C. equisetifolia* was brought to India from Thailand as fuel for the tea-drying industry (U.S. National Research Council 1984). The role of these novel hybrids in *Casuarina* invasions has not yet been investigated.

In Florida, a proposal was put forward for a licensed nursery to provide only male plants for establishment around citrus groves and in addition, include a tax per

tree which would supply funding for the control of *C. equisetifolia* and/or *C. glauca*. Growers would obtain permits from the Department of Environmental Protection (DEP) (as opposed to delisting the species) as casuarinas are prohibited. However, members of the Florida Exotic Pest Plant Council (FLEPPC) were concerned that introgression may become problematic as male trees present a large reservoir for hybridization. Novel *Casuarina* hybrids in Florida have no co-evolutionary history with any insects or diseases, which may be problematic for biological control efforts (Gaskin et al. 2009). Although fully sterile cultivars may alleviate any hybridization concerns, they would take time to develop and this does not resolve the biocontrol conflict.

Impacts of casuarinas in their new ranges

Casuarinas are early-successional and fast-growing species of extreme abiotic conditions (sandy, nutrient-poor soils), and are tolerant to extremes of soil moisture (from very dry to inundated). They are able to tolerate sites with relatively high salinity, low soil fertility and arid conditions. As a result, open, sandy habitats particularly along coastlines in which disturbances have occurred, are particularly susceptible to invasion. These trees have an enormous reproductive capacity due to wind-dispersed seeds that germinate easily to form dense seedling banks and eventually monotypic stands (Kueffer and Lavergne 2004; Wheeler et al. 2011). The habitats of invaded areas are dramatically altered as native plants are overwhelmed by the rapid growth, dense coverage, and thick litter accumulation (Hammerton 2001). Dense shade combined with allelochemical leachates result in a reduction in germination and establishment of native vegetation (Smith 1998; Weber 2003)—providing support for the novel weapons hypothesis (Lamarque et al. 2011). Casuarinas also promote coastal erosion as their shallow roots and tall canopies result in trees being blown over during hurricanes (Austin 1978; Deaton 1994; Swearingen 1997; Hammerton 2001; Sealey 2006). They are known to reduce small mammal populations (Mazzotti et al. 1981) and interfere with the nesting of beach-dwelling reptiles such as the loggerhead and green sea turtles, and the American crocodile (Klukas 1969; Doren and Jones 1997). Large-scale plantations of *C. equisetifolia* established on the coast of India negatively impact the nesting of olive ridley turtles along the Northern Tamil Nadu Coast (Chaudhari et al. 2009). Subramanean and Reddy (2010) revealed that the average population abundance of the sand skink (*Eutropis bibronii*) on the coast of India was significantly reduced by *C. equisetifolia* plantations. Massive plantations may also restrict sand dune formation - an integral part of seashore topography and beach ecosystems (Chaudhari et al. 2009). Snyder (1992) reports that the dense roots of casuarinas reduce soil moisture and damage drains, piping and paving. *Casuarina equisetifolia* has been shown to reduce insect species richness and alter species composition (Sugiura et al. 2013). A recent study conducted by Hata et al. (2012) on Chichijima Island in the subtropical Ogasawara (Bonin) Islands showed that litter decomposition of *C. equisetifolia* may alter nitrogen cycling in invaded forest ecosystems.

Casuarina as a model group

Information summarized in this paper shows that casuarinas share similar drivers of invasion success with other important model groups of woody plants such as Australian acacias, *Eucalyptus* and *Pinus*. The link between planting intensity and degree of invasion in casuarinas resembles that of Australian acacias and eucalypts. As with Australian acacias (Castro-Díez et al. 2011) and eucalypts (Rejmánek et al. 2005), but unlike pines (Richardson et al. 1994), propagule pressure explains much more of the variance in observed invasiveness between *Casuarina* taxa than any known combination of life-history traits. Like Australian acacias (Hui et al. 2011), *Casuarina* species with large native ranges are most likely to be introduced and become naturalized (Fig. 4a). As with Australian acacias and eucalypts, casuarinas exhibit little trait variation and similar traits are shared with each of these model groups, enhancing their invisibility (Table 3). These include: symbiotic associations; fast growth; the ability to grow on low nutrient, highly disturbed soils; intra-specific hybridization between mixed genetic entities in the invasive range. As is the case with alien trees of other taxa (e.g. Kull et al. 2011 for Australian acacias), the number of uses for casuarinas is continuously increasing while the perceptions of alien *Casuarina* species by human

societies differ markedly between regions of the world, which in some cases has led to complex conflicts of interest (Boxes 1, 2). Importantly, casuarinas differ from other model groups in that they invade habitats not invaded by most other invasive woody plants—making this group functionally unique.

Evolution of management approaches for invasive casuarinas

Trees introduced around the world for forestry and agroforestry are predominantly selected for their rapid growth, tolerance of a wide range of conditions, and abundant fruiting and/or seed production (Richardson et al. 2004). These factors can also influence the likelihood of future problems with invasive trees, and so need to be explicitly considered in management schemes (Richardson and Rejmánek 2011).

A range of control methods have been proposed to manage invasive *Casuarina* species. In Florida (USA), Hammerton (2001) and Weber (2003) found fire to be effective for the control of *C. equisetifolia* and *C. glauca*, but only in areas of high density under dry conditions. The trees have some protection from high-intensity fires as understorey vegetation is generally minimal (Smith 1998). *Casuarina equisetifolia* has been noted to recover partially after fire from the basal roots, although the coppicing ability of this species is poorer than for species such as *C. glauca* (Smith 1998). To reduce opportunities for the colonization of *C. equisetifolia*, Swearingen (1997) and Weber (2003) recommend the immediate removal of fallen leaves, cones, seeds and saplings. To avoid the spread of *C. cunninghamiana* along watercourses, Merwin (1989) suggests avoiding planting along riparian corridors. Elfers (1988) and Swearingen (1997) suggest that habitat disturbance should be minimized to reduce opportunities for *Casuarina* colonization and when habitats are disturbed, immediate replanting with native vegetation is required. Control efforts that target the reproductive structures and saplings could reduce the spread of casuarinas into natural areas without affecting their horticultural value. Pemberton (1996) suggests *C. equisetifolia* to be an excellent candidate for biological control because of its large native range, lack of congeners native to its invasive range, and the availability of promising natural enemies. Control methods have been hampered by conflicts of interest regarding perceived uses (see Box 1). For example, on Sanibel Island off the coast of Florida, efforts to remove monotypic stands of casuarinas to re-establish native plant communities and wildlife habitats have been met with intense emotional resistance, including death threats to land managers (Loflin 2004).

In South Africa, *C. cunninghamiana* and *C. equisetifolia* are declared as Category 2 invaders by the Conservation of Agricultural Resources Act, 1983 (Henderson 2001; Henderson 2006). This means that a demarcation permit is required to import, possess, grow, breed, move, sell, and buy the species. Also, no permits are issued for planting of casuarinas in riparian zones. In the Cayman Islands, an immediate importation ban has been implemented for *C. equisetifolia* where control methods, feasibility studies and cost analyses are to be conducted to determine the most appropriate management options for this species. Remote sensing techniques are soon to be implemented to help assess the impact and spread/control of *C. equisetifolia* in the Cayman Islands. Wheeler et al. (2011) propose that the most cost-effective and sustainable management method of casuarinas in Florida lies in a comprehensive integrated control strategy involving safe biological control as a major priority. This management method not only decreases pesticide exposure to humans but can be highly effective (Nel et al. 2004).

Management should be addressed through an ecosystem approach whereby holistic decision-making is implemented. The spatial dimensions of ecological and evolutionary processes or future land-use pressures need to be addressed before conservation planning commences. An assessment of conservation priorities for each region is required. Stakeholder engagement and communication, monitoring, and adaptive management are needed. The solution to problems caused by casuarinas lies in integrating various control methods.

Priorities for future research

Work is needed to improve our understanding of the global distribution of the genus, taxonomic issues, and the many dimensions of interactions between casuarinas and biotic and abiotic factors in their new ranges.

We need to understand the importance of mutualisms between *Casuarina* species and soil biota in mediating naturalization, invasion and impacts. Further research is needed to determine the extent of hybridization in the native and adventive ranges of the genus, and the potential role of this factor in mediating invasions. Our review has shown the importance of macroclimate in *Casuarina* invasions (Fig. 3d; Appendix S2 in Electronic Supplementary Material)—all major invasions of casuarinas have occurred in regions with similar climatic conditions to those that exist in the native range of the genus. Further work to determine microclimatic and microsite requirements of different taxa may well shed light on why certain species have not become widely naturalized or invasive in some areas predicted as climatically suitable. The structure and functioning of biological systems both influence and are influenced by the balance of carbon:nitrogen:phosphorus (C:N:P) ratios between organisms and their environment (González et al. 2010). The ecological stoichiometry of invasive organisms across gradients of nutrient availability remains largely unexplored. As ecosystem resource availability, organism nutrient requirements, and individual competitiveness for resources may be the main interacting mechanisms explaining invasion success, it would be interesting to determine whether C:N:P stoichiometry constrains key physiological and ecological processes, ultimately predicting invasion success in casuarinas.

Various approaches for managing invasive casuarinas have been tried in different parts of the world. Successes and failures need to be comprehensively reviewed to compile guidelines for best-management practices in different situations. Different environmental and socio-political situations produce different categories of conflicts of interest. Useful approaches for dealing with these are emerging following trial and error in different settings. Again, lessons must be learnt and guidelines for innovative solutions need to be compiled. Biological control holds much promise.

Conclusions

Casuarinas have been widely planted by different stakeholders for a variety of reasons, but rarely for commercial purposes. They exhibit similar behaviour to other model groups of trees. For example, like Australian acacias and eucalypts, the extent of invasions is positively correlated with the native range size of *Casuarina* taxa. Invasion success is strongly linked with propagule pressure (as reflected in crude proxies such as coverage in the forestry literature). Like Australian acacias, but unlike pines, they show very little trait variation, and invasiveness cannot be explained on the basis of life-history traits. Casuarinas differ by invading different habitats to most other invasive woody plants (e.g. acacias, eucalypts and pines). A range of management approaches have been tried with varying levels of success in different parts of the world. A substantial invasion debt exists and attention must be devoted to planning to deal with new invasions that will arise in many parts of the world. As with other model groups (e.g. Wilson et al. 2011), lessons can be learnt from regions with a longer history of introduced casuarinas.

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